

Location of terrestrial and aquatic study sites.

The Structure of the Herpetofaunal Assemblage in the Douglas-Fir/Hardwood Forests of Northwestern California and Southwestern Oregon

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Abstract

Terrestrial and aquatic herpetofauna were sampled by three methods, time-constrained searches, pitfall traps, and areaconstrained searches from 1984 to 1986 in northwestern California and southwestern Oregon. The 54 terrestrial and 39 aquatic study sites were in Douglas-fir/hardwood forest stands that ranged in age from 30 to 560 years. Results of these surveys are presented in terms of species richness, equitability, relative abundance, relative biomass, and macrohabitat and microhabitat associations.

Although species richness did not differ among forest ageclasses, the composition of the herpetofauna was notably different. Old and wet sites had proportionately more amphibian species, and young and dry sites had proportionately more reptile species. Terrestrial salamanders were more abundant on old-growth than on young sites. We also found that structural components associated with older forests were the best predictors of increased numbers of salamanders. Analyses of microhabitat associations indicated that large, well-decayed logs were the most heavily used woody debris, though use of particular size- and decay-classes varied among salamander species.

Harvesting forests without immediately affecting herpetofauna is probably not possible; however, strategies can be developed to minimize long-term adverse effects. We provide a summary of management recommendations designed to assure long-term viablity of herpetofauna in areas subject to logging.

Introduction

Old-growth forests are a unique and complex ecosystem where many life forms occur in numbers disproportionate to their occurrence in other parts of their range (Thomas and others 1988), but the nature of the ecological dependencies (Ruggiero and others 1988) between these species and the ancient forest ecosystem are only beginning to be understood. More knowledge about the spatial and temporal distributions of species in old-growth and in younger natural and managed

forests, and an understanding of habitat requirements and ecological interdependencies are required to make sound decisions that assure healthy forests in the future.

We describe the species composition and relative abundance of members of the herpetofaunal assemblage in the southern portion of the Douglas-fir region, with a focus on how presence and abundance are related to forest age and structural aspects of the forest habitat.

Heatwole (1982), in a review of available literature on the structure of temperate and tropical herpetofaunal assemblages, noted how little is known about them and their relation to the larger community of organisms that constitute a complete ecosystem.

Pough (1980, 1983) outlined some of the unique adaptations of herpetofauna that illuminate their critical role in ecosystem dynamics and place them in a larger ecological context. Their small body size and elongate body form, energetically unfeasible for endotherms, permits them to use space and exploit food resources unavailable to other vertebrates. Their ectothermic nature facilitates a life of low energy demand. They are better suited than endotherms to periods of limited food, water, or oxygen. Endotherms are generally viewed in terms of the energy they consume, but reptiles and amphibians are more realistically considered in terms of the biomass they produce and make available to other trophic levels (Pough 1980: 104). These small vertebrates comprise an essential trophic level in the ecosystem, where invertebrate biomass is converted to vertebrate biomass far more efficiently than by endotherms. Pough, comparing the efficiency of secondary production of endotherms and ectotherms, noted that the "...net long-term conversion efficiencies of amphibians and reptiles are many times greater than those of birds and mammals. The ecological significance of this efficient biomass production is enormous" (Pough 1980: 102).

Methods Study Area

The study was conducted in Douglas-fir/hardwood forests of the Klamath Mountains and Coast Range of northwestern California and southwestern Oregon; the southern portion of the Oregonian Province (Udvardy 1975). Fifty-four terrestrial study sites, ranging in size from 21 to 150 ha, and 39 aquatic study sites (15-m lengths of second- or third-order streams) were sampled (see frontispiece and appendix table 9). For site selection procedures see Bingham and Sawyer (this volume). Forests at the terrestrial sites ranged in age from 40 to 450 years; forests at the aquatic sites ranged in age from 30 to 560 years.

Herpetofauna Sampling

Four methods were used to sample the species composition, abundance, and biomass of the herpetofauna: timeconstrained searches (timed searches), pitfall traps (pitfall), area-constrained searches (area searches), and opportunistic observations. These methods are described in more detail elsewhere (Bury and Raphael 1983, Corn and Bury 1990, Raphael and Rosenberg 1983, Welsh 1987). Timed searches recorded the search effort of two to three persons while they moved about the forest at random examining all microhabitats encountered, raking through litter, turning rocks and logs, tearing open decomposed logs, probing in vegetation, and so on. The clock was stopped when animals were encountered and while data were gathered. Our timed searches differed from those of Corn and Bury (1990) in that we searched seeps and springs in addition to rocks, logs, bark, and litter. The **pitfall** method consisted of trap grids with 36 traps spaced at 15-m intervals in a 6 x 6 arrangement. Traps were made of two, number 10 tins taped together and buried with the lip at the groundline and concealed by a cover of bark or cedar shake propped above the ground.

Terrestrial sites were sampled with timed searches, pitfalls, and opportunistic observations. We conducted four person-hour timed searches on each of 54 sites from April to June of 1984 and 1985, and on a subset of 30 sites from April to May of 1986. Our combined effort for timed searches totaled 552 person-hours. We ran 36-trap pitfall grids on 49 sites in October and November of 1984 for 50 nights and October of 1985, for 30 nights. The total pitfall effort equaled 141,120 trap-nights. Twenty-six amphibians and reptiles were recorded by opportunistic observation during sampling for other vertebrate groups or while vegetation data were collected.

Area searches were only done at aquatic sites. Our sampling of aquatic habitats consisted of area-constrained searches of 39 secondor third-order streams (Strahler 1952) on or near the terrestrial sites. We selected three 5-m reaches 1 to 3 m wide along each stream by walking 50 m upstream from the nearest trail or road access for the first reach, and 50 m from the top of the previous reach for subsequent reaches. Stream searches occurred during the summers of 1984 and 1985. The method consisted of mapping each reach to scale in order to plot captures, then methodically and sytematically searching all substrates, with catch nets placed downstream to capture dislodged animals.

Measurements of Forest Landscape, Structure, and Composition

Forest age- and moisture-classes-Sites were grouped into three forest age-classes: young, mature, and old-growth; and old-growth sites were classified into three moisture-classes: wet, mesic, and dry. Forest age was determined by tree

coring, ring counts, and accessing structural characteristics (Old-Growth Definition Task Group 1986). An average of three Douglas-fir trees in the dominant size-class were cored on each site (Bingham and Sawyer, this volume). Age of trees on young sites ranged from 24 to 99 years, on mature sites from 100 to 200, and on old-growth sites >200 years.

Eight of the young forest stands that we sampled had been logged, and three were naturally regenerated after fire. All mature sites were unmanaged. Moisture classification of old-growth terrestrial sites was based on mean percentage cover values and the absolute constancy of particular shrub and herb species (B. Bingham, pers. comm.). Only the old-growth mesic sites were used for analysis of the terrestrial herpetofauna relative to forest age-class.

Landscape and macrohabitat variables-We use the term landscape to describe variables that incorporated a broad spatial scale (for example, elevation and distance from the coast). We used the term **macrohabitat** for aspects of forest structure and composition in general proximity to where animals were sampled.

Plant species composition, structural features, and forest age on terrestrial sites were gathered from three to five, 0.1-ha circular plots in accordance with the methods described in detail in Spies and others (1988) and Bingham and Sawyer (this volume). All dead and down woody material with a diameter ≥ 10 cm was measured. Values were averaged among plots at each site and the means used to represent that variable for the entire site. These data are reported as macrohabitat associations.

Microhabitat variables-With each timed-search capture we recorded type of substrate, vertical postion relative to that substrate, the width and length of substrate objects (for example, rocks, logs, or bark slabs), and the decay state of logs and snags under 5 categories of decay from sound to rotten (Maser and others 1979). Decay-class 1 was defined as a newly fallen tree with intact bark, limbs, and twigs. Decay-class 2 logs were sagging slightly, had intact bark, with some large branches, but no twigs. Decay-class 3 logs were sagging near the ground, with sloughing bark and no large branches. Decay-class 4 logs were completely on the ground, had little or no bark, and the wood was punky. Decay-class 5 logs are well-decayed with soft, powdery wood and massive invasion of roots and seedlings.

We estimated relative abundance of downed woody material by size (based on surface area) and decay-class for our sites by pooling data across vegetation sampling plots within the same stands sampled for herpetofauna (data from B. Bingham). These estimates included only woody material,

not bark, and were calculated separately for hardwood and conifer species. These aspects of the habitat are reported as **microhabitat** associations, and the data are presented as frequencies of occurrence.

Sites Used for Analyses of Landscape and Habitat Parameters

We used data from 42 terrestrial forest sites to compare species richness, species equitability, relative biomass, relative abundance by forest age- and moisture-class, and structural aspects of habitat use. We omitted nine higherelevation, white fir-dominated sites and three sites on serpentine soils because they differed greatly from our remaining sites (appendix table 9). The high-elevation sites were at the upper limit of the range of Douglas-fir and contained a depauperate herpetofauna; the three serpentine sites were open, dry, and brushy with abundant lizards, characteristic of early successional clearcuts. Of the 42 sites, half occurred in the Coast Range (coastal area) and half were inland in the Klamath/Siskiyou Mountains (inland area) (appendix table 9). Differences in species numbers and relative abundance of the total herpetofauna, salamanders, frogs, and reptiles, among forest age- and moisture-classes, were analyzed by geographic area (coastal vs. inland). Al-though the coastal and inland sets of sites also showed a latitudinal gradient, most of the species we examined range across this gradient, therefore, we assumed no effect.

We used 39 stream sites for analyses of the aquatic herpetofauna relative to forest age and habitat variables (appendix table 9). Captures from all three reaches on each stream were totaled for this analysis.

Statistical Methods

No significant differences were found between years for num-bers of captures per site for either the pitfall or timed-search data (Welsh and Lind 1988) so we combined years for these data. Comparisons of mean species richness among forest age-classes were based on the combined pitfall and timed-search data. We used mass data taken during pitfall sampling to compare biomass among forest age- and moisture-classes. In all other analyses of terrestrial herpetofauna we used data from the timed searches.

We tested the null hypotheses of equality of animal (or species) abundance and biomass among forest age- and moisture-classes by geographic area (coastal and inland), and a lack of association between numbers of animals and habitat variables.

We used a 2-factor analysis of variance (ANOVA) to test for differences in species numbers and relative abundance of higher taxa (orders) among age- and moisture-classes in each area (Dixon 1985:BMDP, 2V). Analysis of the relation of individual species to forest age- and moisture-classes were

restricted to those that were found on at least one-third of sites. We incorporated results from an earlier analysis of these data where relationships with forest age- and moisture-classes within and among coastal and inland areas were examined using one-way analysis of variance followed by multiple comparisons (Welsh and Lind 1988). Two species were restricted primarily to either our coastal (California slender salamander) or inland area (Del Norte salamander); their relations to habitat were analyzed only within the appropriate area.

We used Jaccard's similarity coefficient to compare species composition among forest age- and moisture-classes (Sneath and Sokal 1973: 131):

$$S_j = \frac{a}{a+b+c} ,$$

in which, for any two classes, a = number of species in common, b = number of species in the first class only, and c = number of species in the second class only.

Mean biomass for the most common species and higher taxa is reported by forest age-class (coastal and inland areas combined), based on combined fall pitfall samplings from 1984 and 1985-a total of 115,200 trap-nights. We have no way of estimating the actual area sampled by our pitfall grids; however, we assumed that they sampled the same area on all sites regardless of slope or topography. We emphasize that these are not density data. We recognize that many species are not effectively sampled by pitfalls (for example, snakes, clouded salamanders, and treefrogs) and we do not assume, even for those species sampled effectively, that all individuals in the grid area were captured. We present these data as relative biomass. We used a 1-factor analysis of variance (ANOVA) to test for differences in biomass among forest age- and moisture-classes (Dixon 1985:BMDP, 1V).

Correlation and all-possible-subsets regression analysis were used to examine the relationships of the herpetofauna to forest vegetation, structure, and landscape characteristics (Dixon 1985: BMDP, 9R; Neter and others 1989). Forest age and geographic area (distance from coast) were included as continuous variables in this analysis. We analyzed a total of 36 biologically relevant variables relative to captures per personhour (timed search) of salamanders (all species combined), reptiles (all species of lizards and snakes combined), and the four most abundant species of salamander. We selected the 36 variables from an independently derived data set of over 60 measures of forest structure and composition (Bingham and Sawyer, this volume) that we judged biologically relevant to the herpetofauna, and that reduced redundancy (such as selecting hardwood log volume over hardwood log

weight). All-possible-subsets regression was performed on subsets of 15 variables that were most highly correlated with each species or species group but that were not highly intercorrelated (R < 0.80). For each species or group, we report the best univariate and multivariate models with up to five variables, based on maximum adjusted R^2 .

Chi-square goodness-of-fit tests were used to examine the relation between the size, type, and decay-class of downed wood available and the microhabitat associations of the total herpetofauna and selected salamander species.

We emphasize that our inferences are drawn from observations and not experimental manipulations. Although our results are described in the context of hypothesis-testing, our study was primarily exploratory. Because the total number of sites we sampled in each age- or moisture-class was small, we caution against broad inferences. We report actual P-values for our analyses so that readers may judge the level of significance of any particular test result. For purposes of discussion, we use alpha level = 0.05 to indicate significance.

Results and Discussion

Composition of the Herpetofauna

We captured 6419 individuals by all sampling methods combined from the 54 terrestrial and 39 aquatic sites; 97.6 percent were amphibians and 2.4 percent reptiles (table 1). Most captures (88.1 percent) were salamanders, clearly the dominant group among the forest herpetofauna of this region. Bury and Corn (1987), using pitfall/drift-fence arrays in similar forested habitats in the Oregon and Washington Cascades, also found salamanders to comprise a high proportion (51.9 percent) of the herpetofauna. Their data also indicated a high proportion of frogs (42.5 percent) but most of these captures resulted from intercepting groups of dispersing young-of-theyear at a few stands. Using these data to estimate the relative abundance of frogs in the Cascade forests would probably give inflated values, although we would expect frogs are probably more abundant there than here because of the higher and more consistent precipitation in Oregon and Washington.

We suspect that our sampling regime probably underestimated the reptile component of the herpetofauna because of timing. The timed searches were performed in early to midspring, and the pitfalls were run in mid- to late fall corresponding with the fall rains. Both periods would favor the capture of amphibians, but are, respectively, early and late for the best reptile sampling. Combining total captures from our timed-search and pitfall data, we found 2.4 percent were reptiles. Bury and Corn (1987) ran their arrays from late

Table 1-A comparison of numbers of captures by order for herpetofauna collected by 4 sampling methods in Douglas-fir/ hardwood forests of northwestern California and southwestern Oregon from 1984 to 1986

			Taxa			
Method	Sala- manders	Frogs	Lizards	Snakes	Turtles	All species
Pitfall traps Time-	1580	48	13	1	0	1642
constrained searches Area- constrained	3156	49	95	29	0	3329
aquatic searches	914	508	0	0	0	1422
Opportunistic observations	8	4	4	9	1	26
All methods combined Percentage	5658	609	112	39	1	6419
of total	88.1	9.5	1.7	0.6	< 0.01	100

May through the dry summer months and into the fall; they reported 5.6 percent of captures were reptiles. Also, they used funnel traps with their pitfall arrays, which significantly increased their capture of snakes.

Relations of the Herpetofauna to Forest Age, Moisture, and Geographic Area

Species richness and species similarity-Combining all methods, we found 31 species, 16 reptiles and 15 amphibians, on the 54 terrestrial and 39 aquatic sites (table 2); the number of species per site ranged from 1 to 13.

Analysis (ANOVA) of numbers of terrestrial species among geographic areas and forest age- and moisture-classes for 42 terrestrial sites (appendix table 9) indicated no significant differences in species richness among age- or rnoistureclasses, but a significant difference between coastal and inland areas and a significant interaction effect between forest age and area (table 3). We found greater species richness in the Coast Range. Four of the five species detected in the coastal area but not inland (four snakes species) are known to occur in the vicinity of our inland sites. Only the fifth species, the arboreal salamander, has not been reported from this part of California (Stebbins 1985). Consequently, differences in geographic areas do not appear to reflect true biogeographic differences but are probably best explained as an artifact of the difficulty of sampling for snakes (Welsh 1987, Welsh and Lind 1988). The significant interaction effect between forest age and area results from detecting more species in the mature age-class in the coastal area only. We consider that the greater richness found on the coastal

mature stands is a result of these sites being generally closer to ponds and streams than other sites. This proximity to riparian areas tended to increase the number of species (particularly amphibians) detected relative to sites farther from water.

Although we did not find significant differences in species richness among forest age- or moisture-classes, we did find notable differences in species composition. Using presence-absence data, we calculated Jaccard's similarity index for 10 randomly selected sites in each forest age-class. These results (table 4) indicated higher similarity among species for the mature and old-growth sites and lower similarity between the young sites and both of the older age-classes.

These differences among age-classes are attributable to the loss, after logging, of certain amphibian species that occur in the older age-classes and the addition of several lizard species that prefer the open, drier, and warmer areas resulting from clearcut logging. Bury and Corn (1988a), Raphael (1988c), and Raphael and Marcot (1986) also found more lizards in early successional stages after timber harvest.

Using the similarity index for four randomly selected sites in each moisture-class indicated lowest similarities between the wet and dry sites. Differences in species composition among moisture-classes are also attributable to amphibian species being replaced by reptile species on the relatively more xeric and generally more open old-growth dry sites (table 4).

Species equitability-We examined species evenness or equitability by plotting the numbers of captures for the 10 most abundant species vs. species rank, with data (timed-search) from 10 sites in each forest age-class (only the mesic sites from the old-growth set). We ranked the species from most to least abundant along the x-axis. Results indicated that the herpetofaunal assemblage of this area, like other herpetofaunal communities both temperate and tropical (Scott 1982), is dominated by a few species and hence displays low equitability (fig. la). We found little difference among forest age-classes. A similar analysis for four randomly selected sites in each old-growth moisture-class indicated no apparent differences (fig. lb).

Relative abundance-Analysis (ANOVA) of the number of captures (timed-search data-total herpetofauna) by geographic area and forest age- and moisture-class indicated significant differences in total numbers of individuals among forest age-classes (table 3). In a previous analysis of the same data, we found that these differences were significant only between the young and the old-growth sites (old > young, P < 0.05: Welsh and Lind 1988) but not between the two older age-classes.

Table 2-Total captures from all sampling methods and summary of analyses of relative abundance by forest age-class of herpetofaunal species in Douglas-fir/hardwood forests of northwestern California and southwestern Oregon

Mean relative abundance among forest age-classes a, c Sampling Total captures b method(s) a P-value d Species Young Mature Old Frogs and toads 501 Tailed frog AC,PF,TC,OP 0.111 0.555 0.810 0.001 A Western toade PF,TC 4 2 1 Pacific treefrog .049 TC,PF,OP 55 .166 .117 .366 Foothill yellow-legged frog PF,AC 48 .058 .579 .392 .316 Red-legged frog^e OP 1 1 Salamanders Northwestern salamander^e PF,TC,OP 1 3 2 6 Pacific giant salamander AC,PF,TC 19.2 18.1 25.67 .254 B 936 .001 B Olympic salamander TC,AC,OP,PF 48 .000 .038 .192 Roughskin newt TC,PF,AC 97 .038 .140 .192 .377 Del Norte salamander^f TC,PF 471 .396 2.278 .016 B .278 Ensatina TC,PF 2751 2.265 2.595 4.508 .036 Black salamander TC,PF,AC 62 .099 .121 .050 .701 .390 Clouded salamander TC,PF,OP 240 .496 .725 .495 0 Arboreal salamander^e PF 0 1 1 California slender salamander TC,PF 1046 5.533 5.542 .014 2.718 Turtles Western pond turtle^e OP 1 0 1 0 Lizards Western fence lizarde TC,PF,OP 1 4 26 21 Sagebrush lizarde TC, 14 0 0 14 20 7 12 Western skinke TC,PF 1 Southern alligator lizard^e TC4 0 1 3 Northern alligator lizard .095 .042 .239 TC,PF,OP 48 .167 Snakes Rubber boae TC 1 0 0 1 Sharptail snake^e TC,OP 10 1 1 8 0 7 Ringneck snake^e TC 11 4 Racere TC.OP 3 2 0 1 0 0 California mountain kingsnake^e TC 1 1 Common garter snake^e TC0 0 1 1 TC 2 Western terrestrial garter snake^e 2 0 0 Western aquatic garter snake^e TC 1 0 0 1 Northwestern garter snake^e TC,PF 5 2 2 1 0 3 Western rattlesnake^e OP 4 1

^a Data from 1st method listed were used to calculate mean relative abundance and for statistical tests: AC, area-constrained search (aquatic sites only); PF, pitfall traps, TC, time-constrained search OP, opportunistic observations (terrestrial sites only).

^b Data were from 54 terrestrial sites and 39 aquatic sites.

^c Tests based on 42 terrestrial sites (only old-mesic sites were used for age analysis) or 39 aquatic sites (9 young, 9 mature, and 21 old). Young means <100 years old; mature, 100-200 years; old, >200 years old. Some results were previously reported in Welsh and Lind (1988) and Welsh (1990).

^d P-values are from analysis of variance (no letter), Tukey tests (proportions) (A), or regression analysis (B). A dash indicates no test was performed.

^e These species are too uncommon for subsequent analysis; actual captures are reported for these species.

f Sites used for forest age analysis were those within the geographic range of the species.

Table 3--F-statistics and P-values from 2-factor analyses of variance of species richness (timed-search and pitfall data) and relative abundance of higher taxa of herpetofauna (timed-search data) by forest age- and moisture-class in coastal and inland areas

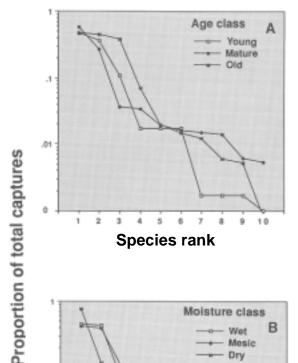
Group definition	Forest age	Area	Inter- action	Forest moisture	Area	Inter- action
Total number						
of species	1.48	12.83	3.36	0.75	0.50	2.98
	(.25)	(.001)	(.05)	(.49)	(.49)	(.08)
Total herpe-						
tofauna ^a	3.33	.00	.24	2.42	1.14	0.85
	(.05)	(.99)	(.79)	(.12)	(.30)	(.45)
All sala-						
manders ^a	3.08	.28	.13	2.24	1.07	.84
	(.04)	(.60)	(.88)	(.14)	(.32)	(.45)
All frogs	1.01	1.48	2.84	7.41	2.33	7.72
	(.38)	(.23)	(.08)	(.006)	(.15)	(.006)
All reptiles	2.68	2.87	.56	2.88	.81	1.76
•	(.09)	(.10)	(.57)	(.09)	(.38)	(.21)

^a Two species of salamander were not included here because of obvious differences in distributions between coastal and inland areas; the California slender salamander occurred primarily on coastal sites and the Del Norte salamander occurred primarily on inland sites.

Table 4-Jaccard similarity index values a for species of herpetofauna in 3 age-classes and 3 moisture-classes of Douglas-fir/hardwood forest

Age-class	Young	Mature	Old growth	
Mature	0.54			
Old-growth	.48	0.71		
Total number of species	$16 (.62)^b$	21 (.62)	15 (.73)	
Moisture-class	Old-wet	Old-mesic	Old-dry	
Old-mesic	.64			
Old-dry	.50	.67		
Total number				
of species	10 (.80)	13 (.69)	17 (.59)	

^a Values are based on data from 10 randomly selected sites in each age-class (mesic old-growth sites only) and 4 sites in each moisture-class, with equal numbers from coastal and inland areas where possible. Greater JSI values indicate greater similarity in species composition.



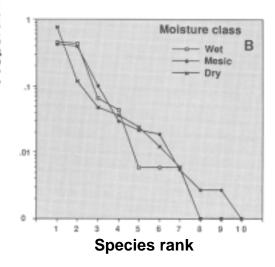


Figure 1-Proportion of total herpetofaunal captures, by ranked species, from (A)10 sites in each forest age-class and (B)4 sites in each forest moisture-class. The first ranked species is the most abundant. Capture data are from timed searches and plotted on a logarithmic scale.

Salamanders (timed-search data, all species combined) showed a significant difference among age-classes (table 3), also occurring in greater numbers on old-growth forest sites (old > young, P < 0.05: Welsh and Lind 1988). Of the eight species of salamanders sampled in sufficient numbers for statistical analyses, half were significantly more abundant on old-growth forest sites: Olympic salamander, Del Norte salamander, ensatina, and California slender salamander (table 2).

b Proportion of amphibians.

Although this analysis failed to detect significant differences among moisture-classes for the total herpetofauna or salamanders (table 3), in a previous analysis of these data, using the Games and Howell modification of the Tukey test, we found significant differences between the mesic and dry categories for both of these groupings (Welsh and Lind 1988).

Frogs detected by terrestrial sampling (timed-search data, all species combined) were not significantly more abundant in any forest age-class (table 3). We did find significant moisture-class effects and moisture-class and area interaction effects, however, these results reflect the fact that terrestrial anurans (mostly Pacific treefrogs) were significantly more abundant on our mesic sites within the Coast Range (mesic > wet, P = 0.02: Welsh and Lind 1988). This result may be due to the fact that the mesic sites were generally closer to appropriate breeding habitat for treefrogs. Terrestrial anurans were absent from most of our inland sites, probably because the inland area is drier than the coastal area. These climatic differences between areas probably account for the significant interaction effect between moisture-class and area indicated for frogs (table 3).

The forest age-class analysis did not yield significant relations for species of terrestrially sampled frogs (table 2). Interpreting our results for the abundance of frogs and aquatic-breeding salamanders relative to forest age- and moisture-class is confounded because we did not gather data on distances from our forest sites to suitable breeding habitat for these species. Proximity of breeding habitat is probably the single most important factor in determining the presence and relative abundance of these species. Bury and Corn (1988a) reported marked increases in numbers of these amphibians on sites near appropriate breeding habitat, regardless of forest age- or moisture-class.

Our aquatic sampling (area searches) detected two species of frogs, the foothill yellow-legged frog and the tailed frog. The tailed frog was significantly more abundant in streams associated with old-growth forests (table 2).

Reptiles as a group did not appear to be significantly influenced by geographic area, forest age, or forest moisture (table 3), but our samples were small for these taxa.

The only reptile species for which we had adequate numbers to compare abundances among forest age-classes was the northern alligator lizard. It was detected in similar numbers in all forest age-classes (table 2).

Table 5-Mean relative biomass, in grams, from pitfall sampling in different age- and moisture-classes of Douglas-fir/hardwood forests in northwestern California and southwestern Oregon

	Young (10) ^d	Mature (11)	Old-wet (6)	Old-mesic (9)	Old-dry (4)
All frogs	1.52 ^b	2.67	0.63	4.63	3.23
	±4.53	±5.46	±1.01	±8.81	±3.73
Salamanders					
Black	.09	3.91	.00	1.11	1.55
salamander	±.28	±11.88	_	±2.25	±3.10
California slender	.69	5.11	.86	5.49	1.20
salamander ^e	±.95	±3.07	±.76	±3.37	_
Pacific giant	18.50	8.90	53.80	18.17	.00
salamander	±37.70	±16.46	±47.90	±28.67	_
Ensatina	70.10	93.00	53.20	81.90	118.80
	±43.90	±81.80	±37.40	±64.80	±82.10
Del Norte	6.41	1.00	8.66	73.80	.00
salamander ^e	±9.40	±2.45	±12.90	±145.60	_
Roughskin	2.86	4.09	2.27	7.82	1.87
newt.	±4.46	±4.69	±5.03	±17.37	±3.75
All salamanders ^d	94.50	112.70	114.00	152.50	122.60
	±67.40	±76.00	±64.30	±116.00	±85.70
All reptiles	1.65	.50	.57	.95	1.47
	±5.22	±1.15	±1.38	±1.95	±1.99

^a Number of sites.

Mean biomass-We found a pattern of increasing biomass of terrestrial amphibian species from young to old-growth forest age-classes (table 5). Because of high variances among sites within both age- and moisture-classes, however, analysis (1-factor ANOVA) indicated only one species, the California slender salamander, to have significantly higher biomass on older stands (F = 6.99, P = 0.009).

Ensatina accounted for 67 percent of the relative biomass (all sites combined) followed by the Pacific giant salamander at 16 percent. Some notable differences were found in some species' relative contributions to abundance and biomass. The Pacific giant salamander had low mean relative abundance (0.182/1000 trap-nights), but its mean biomass exceeded that of the more abundant California slender salamander (1.23/1000 trap-nights) and the Del Norte salamander (3.65/1000 trap-nights) in most forest age- and moisture-classes (table 5). These two smaller salamanders accounted for 1 percent and 9 percent of the biomass, respectively.

^b Mean ±1 standard deviation.

^c Stands within the geographic range only; slender salamander: n = young, 7; mature, 5; old-wet, 3; old-mesic, 4; old-dry, 1. Del Norte salamander: n = young, 3; mature, 6; old-wet, 3; old-mesic, 5; old-dry, 3.

^a Sum of biomass of above 6 species only; incidental records of other species omitted.

Differences between the Coast Range and the Klamath

Mountains-Although we consider the difference in mean number of species between coastal and inland areas (table 3) to be an artifact of sampling difficulties rather than a reflection of true biogeographical differences, we did find some evidence of real differences between these areas. For example, we found significantly more black salamanders and a pattern of higher abundance for many other species in the Coast Range, although differences were not statistically significant for the other species (Welsh and Lind 1988). We think that the explanation for these results lies in differences in the suitability of habitats for the herpetofauna. Progressing from the influences of the Pacific Ocean eastward toward interior California is a pronounced environmental gradient characterized by high precipitation, both rain and fog, and mild temperatures along the coast, to lower precipitation and more extreme temperatures-both highs and lows-farther inland (Kahrl 1979:5, 13). Conditions along the coast create more suitable conditions for forest-dwelling herpetofauna, particularly amphibians, than do conditions inland. This climatic gradient may have affected the number of species (table 3), the increasingly patchy distribution of their populations, and their relative abundance (see below). For example, we found the black salamander on 43 percent of coastal stands versus 19 percent of inland stands (also see Lynch 1981). Either actual densities of individuals of many but not all species are greater in coastal areas, or more equable coastal habitats tend to increase the likelihood of detection of individuals and of less-common species because of more accessible retreats (near or on surface vs. subsurface cover).

Forest Landscape and Habitat Structure: Macrohabitat Associations

Herpetofaunal abundances (timed-search data) were related to macrohabitat characteristics of the forest by using correlation and regression analyses for 36 variables (table 6). We report the five "best" single predictor-variables of animal abundance, and the best multivariate models (up to five variables) for the most common species of salamanders and for salamanders and reptiles as a whole (table 7).

Salamanders-As a group, salamanders were significantly related to macrohabitat variables associated with late-successional stages of the forest (table 7): increasing densities of large trees, particularly hardwoods, and large snags, and a decreasing density of small conifers. Also of importance in predicting salamander numbers were landscape variables (table 6) indicative of relative moisture in the habitat-distance from coast (negative correlation) and presence of seeps. The third type of variable that entered into our predictive models for salamanders were ground layer variables: percentage cover of rock, a significant indicator of protective cover, and percentage vegetation cover from 0 to 0.5 m high.

Table 6-Macrohabitat variables used for multiple regression analysis

Landscape variables

Forest age (years)

Elevation (m)

Solar (KgCal/cm²[Langleys]/year)

Presence of streams

Presence of seeps

Distance from coast

Tree variables

Small conifers (all tree variables are stems/ha)

Large conifers (>80 cm diameter at breast height [d.b.h.])

Small hardwoods

Large hardwoods (>50 cm d.b.h.)

Small trees

Large trees

Basal area conifers (m²/ha)

Basal area hardwoods

Total basal area

Conifer importance (number of stems + basal area)

Hardwood importance

Canopy cover (ocular percentage cover estimate; mean of 3-5 200 m² plots/stand)

Coarse woody debris variables

Large snags (>50 cm d.b.h. & >4.5 m tall)

Small snags

Large conifer logs (>50 cm diameter & >15 m long; pieces/ha)

Small conifer logs

Small hardwood logs

Large logs

Small logs

Large-log weight (metric tons/ha)

Small-log weight

Conifer-log volume (m³/ha)

Hardwood-log volume

Sound-log volume

Decayed-log volume

All-log volume

Ground layer variables

Litter depth (mm; average of 36-60 profiles/stand)

Rock (ocular percentage-cover estimate; mean of 3-5 200 m² plots/stand)

Ferns (ocular percentage-cover estimate; mean of 3-5 200 m² plots/stand)

0-.5 m vegetation cover (ocular percentage-cover estimate; mean of 3-5 200 m² plots/stand)

Vegetation cover was negatively correlated with salamander abundance, but this may be a sampling artifact. Given equal search time on otherwise comparable sites (timed-search method), the site with the thicker understory might yield fewer salamanders because of increased difficulty in finding obscured cover materials (Welsh and Lind 1988).

 $Table\ 7-Results\ of\ multiple\ regression\ analysis\ for\ abundance\ of\ selected\ herpetofauna\ (timed-search\ data)\ relative\ to\ macrohabitat\ variables\ (the\ 5\ best\ single\ variables\ and\ the\ best\ multivariate\ models\ are\ given)$

Variables in model	$\mathbf{C}^{\;a}$	R^2 (adj.)	F	P
All salamanders:				
Large hardwoods	+	0.286	16.22	0.0003
Small conifers	-	.270	15.11	.0004
Large trees	+	.259	14.32	.0005
Distance from coast	-	.222	11.87	.001
Basal area of hardwoods	+	.204	10.77	.002
Small conifers, 0-0.5 m cover		.458	17.07	<.0001
Large trees, distance from coast, 0-0.5 m cover	+,-,-	.519	14.68	<.0001
Large trees, distance from coast, large snag				
numbers, seeps present	toot	.565	13.33	<.0001
Large trees, distance from coast, large snag				
numbers, seeps present, rock	+,-,-,+,+	.603	12.56	<.0001
Ensatina:				
0-0.5 m cover		.232	12.51	.001
Large hardwoods	+	.180	9.32	.004
Seeps present	+	.171	8.85	.005
Small hardwood logs		.150	7.74	,008
Large trees	_	.143	7.33	.010
0-0.5 m cover, large trees	+	.406	13.99	<.000
0-0.5 m cover, large trees, seeps present		.486	12.96	<.000
0-0.5 m cover, large trees, seeps present,	-,+,+	.480	12.70	<.000
distance from coast		612	10.97	- 000
	-,+,+,+	.512	10.97	<.000
0-0.5 m cover, large trees, seeps present,		500	0.00	000
distance from coast, small conifers	-,+,+,-	.523	9.33	<.0001
Del Norte salamander:		257		040
Small conifers		.257	6.89	.018
Forest age	+	.247	6.56	.021
Rock	+	.246	6.55	.021
Basal area of hardwoods	+	.232	6.13	.025
Large trees	+	.226	5.95	.027
Basal area hardwoods, small-log weight	+,-	.491	9.19	.002
Seeps present, hardwood-log volume,				
small-log weight	+,-,-	.668	12.41	.0003
Seeps present, hardwood-log volume,				
small-log weight, rock	++	.803	18.29	<.000
California slender salamander:				
Elevation	-	.693	46.08	<.000
Distance from coast		.449	17.31	.000
Large trees	+	.312	10.09	.005
Rock	+	.201	6.05	.024
Small conifers		.175	5.24	.034
Distance from coast, small trees	-,-	.833	50.74	<.000
Distance from coast, small trees, elevation:		.849	38.48	<.000
California slender salamander (without				
elevation and distance from coast):				
Large trees	+	.312	10.09	.005
Rock	+	.201	6.05	.024
Small conifers		.175	5.24	.034
Large hardwoods	+	.120	3.74	.068
Forest age	+	.077	2.68	.118
Large trees, rock	+,+	.404	7.78	.004
Large trees, sound-log volume, seeps present	+,+,-	.438	6.19	.005
and an entropy promise row volume, propps projecting	1919		0.17	2000

	R^2					
Variables in model	C^{a}	(adj.)	F	P		
Clouded salamander:						
Small-log weight	+	.257	14.18	.0006		
Decayed-log volume	+	.133	6.88	.013		
Canopy cover	+	.119	6.14	.018		
Small conifer logs	+	.118	6.10	.018		
Seeps present	+	.076	4.14	.049		
Small-log weight, canopy cover	+,+	.280	8.42	.001		
Small-log weight, elevation, basal area						
of hardwoods	+,+,+	.294	6.28	.002		
Small-log weight, elevation, basal area						
of hardwoods, solar	+,+,+,-	.331	5.71	.001		
All reptiles:						
Seeps present	_	.102	5.31	.027		
Large snags		.101	5.29	.027		
Elevation	-	.085	4.54	.040		
Canopy cover	_	.085	4.54	.040		
Conifer-log volume	_	.076	4.11	.050		
Large snags, canopy cover	~~	.159	4.61	.017		
Seeps present, solar, conifer importance	-,+,-	.213	4.42	.010		
Small snags, seeps present, large-log weight,						
solar	+	.237	3.95	.010		
Solar, litter depth, seeps present, elevation,						
conifer importance	toooc	.270	3.81	.008		

^a Partial correlation (positive or negative).

Ensatina-We captured more ensatina, by both timed search and pitfalls than any other species (table 2; Welsh and Lind 1988). Significant relationships with large-tree and largehardwood densities (positive correlations) and small conifers (negative correlation) (table 7) are consistent with significantly higher abundances of ensatina on old-growth sites (table 2). Also significant in our predictive models for this species are variables indicative of protective cover: density of small hardwood logs (positive correlation), and vegetation cover from 0 to 0.5 m tall (negative correlation-see explanation above, under salamanders). Presence of seeps, possibly an indication of relatively moister soils, was also important for ensatina. Previously (Welsh and Lind 1988), we found significantly more ensatina in the inland area. The appearance here in two of our models of a positive correlation with "distance from coast" (table 7) is consistent with our earlier result. This finding contrasts with the negative correlation for salamanders as a whole (table 7). Despite its ubiquity in the moist, cool forests of the Pacific Northwest and in contrast to other native salamanders, ensatina appears to have greater tolerance of the higher temperatures and lower moisture that are characteristic of interior forested areas of northern California. This tolerance is further evidenced by its distribution in other parts of California, particularly the Sierra Nevada, and the mountains of southern California (Stebbins 1985).

Del Norte salamander-This species was found primarily on sites in the Klamath/Siskyou mountains, and a subset of sites within their geographic range was used in the analysis (n = 18). Del Norte salamander abundance varied positively with forest age, basal area of hardwoods, and large trees, and negatively with small conifers (table 7), a pattern indicative of late-successional forest. Percentage cover of rock was also important. This species was always found on sites with rocky soils, and most captures occurred in direct association with rock or under woody debris in contact with rock. The reason for the addition of two negatively correlated variables describing downed woody material in the multivariate models for this species (table 7) is not clear.

California slender salamander-This species was found primarily on sites in the Coast Range, and a subset of sites within their geographic range was used in the analysis (n = 21). The greatest amount of variation in numbers was accounted for by the landscape variables of elevation and distance from coast (negative correlations; table 7). A single cover variable-percentage cover of rock-and several variables indicating late-successional forest also proved to be significant. Significance of the late-successional forest variables is consistent with earlier analyses that found the slender salamander to occur in greater abundance on oldgrowth sites (table 2; Welsh and Lind 1988).

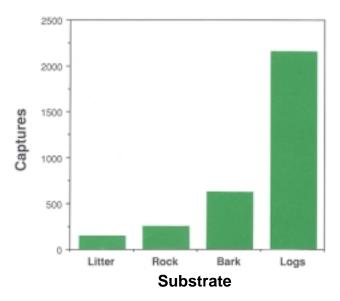


Figure 2-Captures of herpetofauna (all species combined from timed searches) by substrate type.

We performed a second multiple regression on the slender salamander data to determine the importance of forest structural factors apart from the overriding factors of elevation and distance from coast (table 7). The second analysis brought in additional variables that covaried positively with late-successional forest, such as forest age and large hardwoods, but these variables were not significant. The cover variable sound-log volume and the presence of seeps were significant in our second multivariable model, however. Bingham and Sawyer (this volume) found sound-log volume to be greater on old growth than young or mature sites, and the positive correlation with abundance of slender salamanders once again indicates an association with older forests. The negative correlation with presence of seeps is difficult to explain and may be spurious.

Clouded salamander-Our analysis of data for this species indicated an association with cool, moist forest with positive correlations with increasing canopy cover and presence of seeps. Its abundance was also related to decayed woody debris (significant positive correlations with small-log weight, decayed-log volume, and small conifer logs). The remaining variables entering models are consistent with these associations (table 7). The low adjusted R^2 for our best model (0.331) explained less than half the variation in abundance, however.

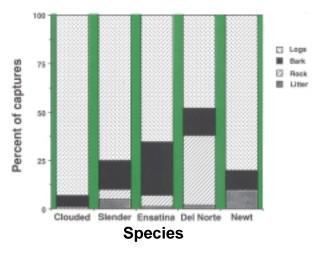


Figure 3-Captures of common salamanders (timed search) by substrate type.

Reptiles-Our analysis of reptiles is based on a total sample of 151 captures of 15 species, including both snakes and lizards (table 2). Lumping such a diverse array of species has obvious shortcomings, but it offers an informative contrast to macrohabitat use by the salamanders which dominate the forest herpetofauna of this region. Five significant variables entered the model; reptile abundance was negatively correlated with all of them (table 7). Collectively, high values of these variables indicated cool, moist, late-successional forests-clearly not optimal habitat for most reptiles. Additional variables that entered the regression models were also indicative of late-successional forests and negatively correlated with reptile abundance. The only variable that showed a positive correlation with reptile abundance was "solar," a measure of incident radiation (Frank and Lee 1966), as would be expected with a group of heliothermic species. The adjusted R^2 for our best model (0.270) indicated these variables explained little of the observed variation in reptile abundance.

Forest Landscape and Habitat Structure: Microhabitat Associations

Substrates-We analyzed all timed-search captures by substrate, combining them into four categories (fig. 2). Of 2769 total captures, 87.5 percent were associated with dead, woody plant material-logs, snags, and bark. We analyzed the distributions of the five most commonly captured salamanders relative to these substrate categories (fig. 3). Ninety-nine percent of clouded salamanders, 89 percent of slender salamanders, 93 percent of ensatina, and 90 percent of roughskin newts were captured in association with dead, woody plant material. The slender salamander was more commonly encountered in the litter layer, and the Del Norte salamander more commonly captured among rocks, than any of the other salamander species (fig. 3).

Table 8-Results (P-values) of chi-square analyses comparing logs where salamanders were captured to the distributions of logs in different size- and decay-classes

			Size-class (conifers) ^b					Size-class (hardwoods)					Size-class (hardwoods)			
Species	1	2	3	4	5	6	7°	1	2	3	4	5	6"	7"	To	
Clouded	***	***	0.35				-		***	0.36	***	***	-		**	
salamander	-	-		+	+			-	-			+				
California slender	***	***	***		***	***	-	***	0.09	.72	0.47	***	_	_	**	
salamander	+				+			+				+				
Ensatina	0.31	+++	**	0.30	***	***	-	***	**	.22	***	***	_	_	**	
					+	+		+				+				
Del Norte	***	***	**		.36	27	-	***	.41	.13	.27	.73	_	_		
salamander	+	-						+								
Total		***	***	.71	***	***	_	***	***	.85	***	***	_	_		
herpetofirma	+				+	+		+			+	+				
	_	3,700.0	y-class (co	inserey	-				1000	y-class (ha	- Inches					
	1	2	3	4	5			1	2	3	4	5				
Clouded		**	***	.25	***				.07	**		.46				
salamander			+					-		-						
California slender	**	***	***	***	.07			***	***	.66	***	.29				
salamander	-							-			+					
Ensatina.	***	***	***	***	.37			***	***	***	***	***				
	-							-			+	+				
Del Norte	.12	***	.05		.13			.12		**	***	***				
salamander												*				
Total	***	***	***	***				***	***	***	***	***				
herpetofauna				+							+	+				

^a Expected values were calculated from an independent data set of structural variables measured on the stands where berpetofaunal sampling occurred. Species captured in significantly greater (+) or smaller (-) numbers than expected for each class are indicated by *'s (* = 0.05 > P > 0.01; ** = 0.05 > P > 0.01;

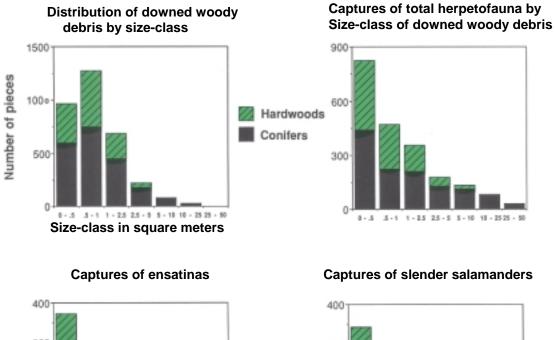
Herrington (1988) reported the Del Norte salamander as essentially restricted to talus habitat. We concur that rocky habitats are important for this species (see macrohabitat section, above), but we believe some clarification is warranted. All of our captures for the Del Norte salamander occurred on sites with talus, rock outcrops, or rocky soils. Within these areas, however, we also found this species using downed woody debris for cover. Sixty-two percent of our captures were associated with such material (fig. 3), and 5 percent were within decayed logs.

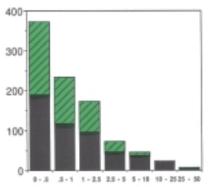
We have almost no knowledge of the importance of belowsurface habitat use for forest salamanders (N. Scott, pers. comm.); however, our data indicate that large numbers of salamanders use the subsurface, surface, and above-surface habitats provided by downed woody debris. Similar results from other studies in comparable habitats (Aubry and others 1988; Bury and Corn 1988a; Corn and Bury, this volume b) support the conclusion that these habitat features are probably essential for many species of forest salamanders. Size of woody debris cover-The highest capture rates of all species combined were in the smallest and the next two larger size-classes of both conifer and hardwood logs (fig. 4). Captures were significantly lower than expected in several of the intermediate size-classes and did not vary from expected captures in others (table 8). The most abundant downed woody materials on our sites were pieces in the 0.5- to 1-m² size-class (fig. 4), but the frequency of captures of herpetofauna for this size-class was significantly less than expected (table 8). Although we captured salamanders in the largest size-classes of both conifers and hardwoods, the independent data set from which we derived our expected values lacked sufficient numbers of logs in these classes to allow for statistical tests (fig. 4, table 8).

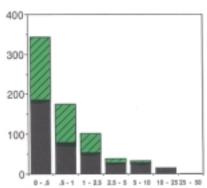
The slender salamander and ensatina occurred in patterns similar to that described for the total herpetofauna (table 8). The clouded salamander, however, apparently chooses the larger classes (table 8), particularly of conifer logs (fig. 4), consistent with the findings of Corn and Bury (this volume b). The

^b Size-classes of downed woody debris are presented in square meters and defined as follows: 1, 0 - 0.5; 2, 0.5 - 1; 3, 1 - 2.5; 4, 2.5 - 5; 5, 5 - 10; 6, 10 - 25; and 7, 25 - 50.

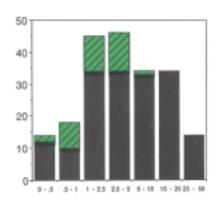
^c Not tested; no expected values available.











Captures of Del Norte salamanders

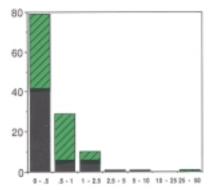


Figure 4-A comparison of the distribution of size-classes of hardwood and conifer downed woody debris (B. Bingham, pers. comm.), with the use of size-classes by the total herpetofauna (timed search) and the five most abundant salamander species.

Del Norte salamander occurred more often than expected under the smallest size-class of both hardwood and conifer debris, less than expected in intermediate conifer debris, and showed no deviation from expected in large conifer and all other hardwood classes (table 8).

Decay-class of woody debris-Our estimates for the amount of downed woody material (logs and branches-snags were not included) by decay-class indicated a nearly normal distribution from sound to rotten, with more conifer than hardwood pieces (fig. 5). Decay-class 3, characterized by logs with bark exfoliating and heartwood beginning to rot, contained the most pieces. In contrast, captures of the total herpetofauna by decay-class indicated significantly more captures than expected for class 4 conifer and class 4 and 5 hardwood logs, and fewer captures than expected in class 1, 2, 3, and 5 conifer logs, and class 1, 2, and 3 hardwood logs (table 8).

The slender salamander and ensatina occurred in patterns similar to those of the total herpetofauna with two differences. Both occurred as expected in class 5 conifer logs, and the slender salamander also occurred as expected in class 3 and 5 hardwood logs (table 8). The clouded salamander showed a strong preference for conifer logs (82 percent of all captures; fig. 5), and was captured more often than expected in decay class 3 (table 8). The Del Norte salamander was captured more often than expected under class 4 and 5 hardwood and class 4 conifer logs, and significantly less often in association with many of the sound-log classes (table 8).

Conclusions

Although we found 31 species of amphibians and reptiles over the course of this study, with 1 to 13 species per site, the herpetofauna of the region demonstrated low equitability, being dominated by a few species of salamanders. Species richness did not differ by forest ageor moisture-class, but species composition did. Several species of amphibian were rare or absent from young sites, while reptiles were relatively more abundant on these sites and on the old-growth dry sites.

We captured over 6400 individuals, of which 97.6 percent were amphibians, with salamanders comprising 88.1 percent. Terrestrial salamanders were more plentiful on old-growth sites, with four of eight species sampled at greater than incidental levels, significantly more abundant on these sites. Concurrently, we found greater relative biomass of amphibians on old-growth mesic sites and greater relative biomass of reptiles on young and dry sites.

We found that structural components (multiple regression analysis; macrohabitat variables) associated with older forests (Franklin and Spies, this volume) were the best predictors of increased numbers of salamanders.

Our analysis of microhabitat associations indicated that large, well-decayed logs, both hardwood and conifer, were the most heavily used downed woody debris. We found that the pattern of use of woody debris varied considerably, both in size-and decay-class, by species of salamander.

Nineteen of the 31 species we detected were captured at incidental levels (table 2). Some of these species may be considered secondary elements of the forest herpetofauna-for example, the sagebrush lizard that invades open areas subsequent to harvesting. Others, however, were captured rarely, either because they were uncommon or because we lacked adequate methods to sample them-for example, snakes. We know little about these species' life histories, their relation with the forest environment, what constitutes a viable population, or how these populations respond to the conversion of old-growth forests to young, managed stands.

Management Strategies To Maintain a Viable Herpetofauna

An increasing body of evidence from research in forested habitats indicates a change in herpetofaunal species composition, reduction of numbers of species, and reduced abundance within species after logging (Bennett and others 1980; Blymer and McGinnes 1977; Buhlmann and others 1988; Bury 1983; Bury and Corn 1988a, 1988b; Bury and Martin 1973; Coin and Bury 1989; Enge and Marion 1986; Gordon and others 1962; Herrington and Larsen 1985; Pough and others 1987; Ramotnik and Scott 1988; Welsh and Lind 1988). Forests cannot be harvested without affecting the herpetofauna, but we believe that it is possible to reduce long-term adverse effects. Area-specific strategies can be developed that take into account the natural history of local species of reptiles and amphibians and the particular habitat requirements of these species. With this knowledge, the timing and potential effects of harvest activities can be modified to ensure minimal impact and thus maintain the long-term viability of the herpetofauna.

Based on data reported here and previously (Welsh and Lind 1988) for northwestern California and southwestern Oregon and summarizing ideas presented by other authors cited above, we propose a four-part strategy to ensure the long-term viability of all elements of the local herpetofauna in areas subjected to logging.

Avoid riparian zones-Riparian zones are often the most species-rich (for all wildlife, not just herpetofauna), and their protection with no-cut buffer zones could maintain source populations and corridors for gene flow that would promote rapid repopulation once regeneration has created suitable habitat in harvested upland areas (see Bury and Corn 1988b; Bury and others, this volume b; Gilbert and Allwine, this volume c).

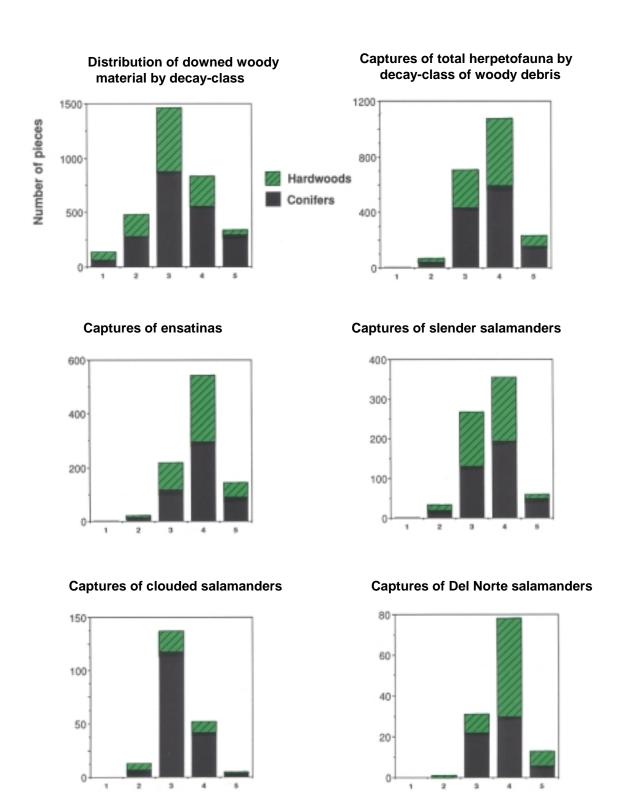


Figure 5-A comparison of the distribution of decay-classes of hardwood and conifer downed woody debris (B. Bingham, pers. comm.), with the use of decay-classes by the total herpetofauna (timed search) and the five most abundant salamander species.

Protect special habitats-Protecting special habitats includes springs, seeps, and other headwater habitats; large rock outcrops; talus slopes; ponds, and unique patches of habitat that are critical to certain highly sensitive species (for example, the red-legged frog, Olympic salamander, tailed frog, and Del Norte salamander) (see also Bury 1988; Bury and Corn 1988b; Bury and others, this volume a, b; Corn and Bury 1989; Gilbert and Allwine, this volume c; Herrington 1988).

Provide microhabitat--For forest herpetofauna, providing microhabitat means managing for downed woody debris. Almost all species of forest herpetofauna use woody debris at some stage, and many species use it throughout their existence, for cover, foraging, or nesting. After logging, an abundant amount of woody debris should be left, in all sizes and decay-classes, including both hardwoods and conifers when present, to facilitate the recovery of the terrestrial herpetofauna and other small vertebrates (see also Aubry and others 1988; Bury and others, this volume a; Corn and Bury, this volume b). The simplest approach is to leave all downed woody debris that was present before harvesting.

Minimize direct logging effects-Restricting tractor logging would minimize compaction of the soil, and cable logging in winter would have far less effect on hibernating herpetofauna (Ramotnik and Scott 1988). As much canopy as possible should be left to prevent drying of the soil and alteration of understory vegetation.

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Appendix

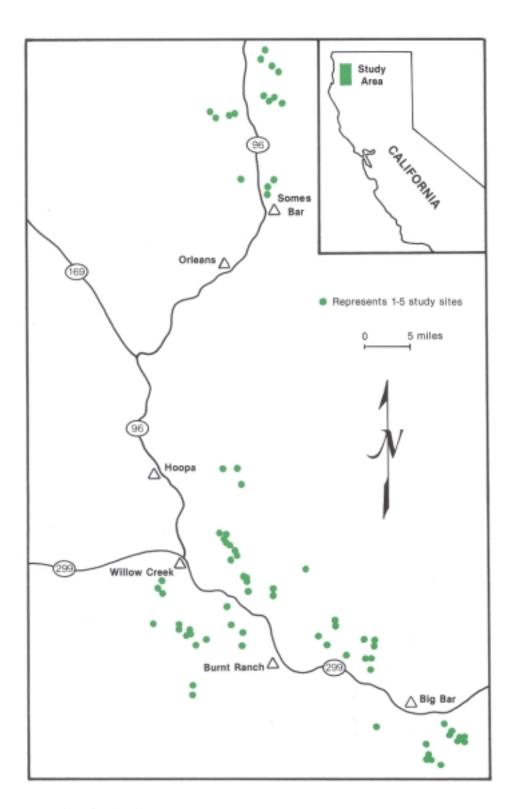
 $Table \ 9-Study \ sites \ in \ mixed \ evergreen \ forests \ of \ northwestern \ California \ and \ southwestern \ Oregon \ (sites \ marked \ with \ an \ asterisk \ were \ included \ for \ total \ capture \ counts \ but \ omitted \ from \ further \ analyses \ see \ text)$

Sites	Age- class ^a	Moistre- class ^{b,c}	Location	County, State d	Elevation (m)	
Terrestrial:						
Inland						
Little Greyback	Y	M	T39S,R6W,S8	Jos,OR	1205	
Tunnel	Ÿ	M	T18N,R4E,S3&4	DeI,CA	624	
Waterman Ridge	Ÿ	M	T7N,R5E,S 15	Hum,CA	633	
*Buck Peak	Ÿ	M	T39S,R6W,S33	Jos,OR	1366	
Althouse	M	M	T40S,R8W,S3	Jos,OR	427	
Brush Mountain	M	M	T6N,R5E,S18	Hum,CA	1050	
Gray	M	M	T5N,R6E,S4&5	Tri,CA	972	
Hennessey Peak	M	M	T5N,R6E,S8&9	Tri,CA	949	
Oregon Caves	M	M	T39S,R6W,S31	Jos,OR	872	
Shelterwood	M	M	TIN,R4E,S34	Hum,CA	1022	
*Left Hand	M	M	T40S,R6W,S23	Jos,OR	1362	
	M	M		Jos,OR Jos,OR	1502	
*Upper Horse	O	W	T40S,R6W,S 16			
Beartooth Mountain			T6N,R7E,S34	Tri,CA	1144	
Brannon East	O	W	T6N,R4E,S13&24	Hum,CA	750	
Cedar Creek	0	W	T7N,R5E,S30	Hum,CA	665	
*California Greyback	0	W	T19N,R6E,S32	Del,CA	1556	
*Frog Pond	O	W	T41S,R7W,S14	JOS,Or	1539	
*Holcomb Peak	O	W	T39S,R6W,S9	Jos,OR	1411	
*Serpentine Wet	O	W	T41S,R9W,S4	Jos,OR	549	
Big Creek-East	O	M	T6N,R7E,S36	Tri,CA	1134	
Clouded	O	M	TIS,R4E,S2	Hum,CA	961	
Ladder Rock	O	M	T8N,R6E,S32	Hum,CA	805	
Spotted Owl	O	M	TIS,R4E,S2&3	Hum,CA	981	
Tish Tang	O	M	T8N,R5E,S35	Hum,CA	680	
Sharber	O	M	T6N,R6E,S7	Tri,CA	747	
*Galleghy Grove	O	M	T41S,R7W,S8,9,17,18	Jos,OR	1334	
*Page Mountain	O	M	T41S,R7W,S8	Jos,OR	1519	
*Serpentine Mesic	O	M	T38S,R9W,S25	Jos,OR	527	
*Skag Hope	O	M	T41S,R7W,S7	Jos,OR	1305	
Happy Camp	O	D	T40S,R7W,S29&30	Jos, OR	1053	
South Fork	O	D	T6N,R6E,S31	Tri,CA	659	
Waters Creek	Ö	D	T36S,R7W,S28,29,32,33	Jos,OR	614	
*Serpentine Dry	Ö	D	T38S,R8W,S29	Jos,OR	544	
Coastal						
Bald Mountain	Y	M	T6N,R3E,S17&20	Hum,CA	846	
Barnes Thirty	Y	M	T22N,R16W,S29&32	Men,CA	467	
Fawn Prairie	Y	M	T7N,R2E,S25	Hum,CA	750	
Homestead	Y	M	T21N,R16W,S13&24	Men,CA	726	
Lord Ellis	Y	M	T6N,R3E,S8&17	Hum,CA	778	
Mud Springs	Y	M	T21N,R15W,S13&24	Men,CA	689	
Seed Tree	Y	M	T14N,RIE,S21&22	De1,CA	120	
Shelterwood Leave	Y	M	T14N,RIE,S27	Del,CA	120	
Elder Creek	M	M	T22N,R16W,S28	Men,CA	555	
Elkhorn Xeric	M	M	T22N,R16W,S17	Men,CA	518	
Fanny's Place	M	M	T22N,R16W,S21	Men,CA	445	
Harwood's 90	M	M	T21N,R15W,S23	Men,CA	695	
White House	M	M	T22N,R16W,S21	Men,CA	427	
Old Growth	Ö	W	T14N,RIE,S21&28	De1,CA	53	
Skunk Creek	Ö	W	T22N,R16W,S29	Men,CA	529	
Standley Grove	Ŏ	W	T21N,R16W,S26	Men,CA	481	
Alpine	ŏ	M	T22N,R16W,S20&21	Men,CA	444	
Elkhorn Hydric	Ö	M	T22N,R16W,S20&21	Men,CA	518	
Fox Creek	Ö	M	T22N,R16W,S17 T22N,R16W,S21&22	Men,CA	543	
Ten Mile Creek	Ö	M M	T22N,R16W,S21&22 T22N,R16W,S15&16	Men,CA	343 445	
Len Mile Creek						

Table 9-continued

Sites	Age- class ^a	Moisture- class ^{b,c}	Location	County, State ^d	Elevation (m)
Aquatic:					
Ammon-North	Y		T5N,R5E,S11	Hum,CA	549
Barnwell Creek	Y		T22N,R16W,S21	Men.CA	427
Bybee Creek	Ý		T19N,R5E,S33	Del.CA	671
Coon Creek	Ÿ		T7N,R5E,S15&16	Hum,CA	213
Four Mile Creek	Ÿ		T6N,R5E,S20	Hum.CA	671
Hawkins Tributary	Ÿ		T6N,R6E,S15&16	Tri,CA	488
Kenny Creek	Ÿ		T21N,R16W,S14&15	Men,CA	472
Sixteen Gulch	Ÿ		T18N,R15W,S31	Men.CA	171
Sugar Creek	Ÿ		T22N,R16W,S29&32	Men,CA	466
Althouse-Main	M		T41S,R7W,S 11	Jos,OR	1341
Althouse-West	M		T41S,R7W,S 16	Jos,OR	1158
Bolan Creek	M		T40S,R6W,S31	Jos,OR	975
Chamberlin Creek	M		T18N,R15W,S27&28	Men.CA	244
Days Gully	M		T38S,R9W,S25&36	Jos,OR	526
Lefthand Creek	M		T40S,R6W,S23	Jos,OR	1361
Limestone Creek	M		T40S,R6W,S21	Jos,OR	1067
McKinley Creek-Upper	M		T22N,R16W,S21	Men,CA	445
Page Creek	M		T41S,R8W,S2	Jos,OR	561
Barney Creek	O		T5N,R5E,S32	Hum,CA	823
Big Creek-East	Ö		T6N,R7E,S36	Tri,CA	1133
Big Creek-Main	Ö		T6N,R7E,S24	Tri,CA	1067
Brannon Creek	O		T6N,R4E,S13&24	Hum,CA	750
Butte Creek	O		TIS,R4E,S2&3	Hum.CA	980
Campbell Creek	Ö		T7N,R4E,S23	Hum,CA	884
Cedar Creek	O		T7N,R6E,S26	Hum.CA	1006
Elder Creek	O		T22N,R16W,S34	Men.CA	533
Elk Creek	O		T40S,R5W,S 12	Jos,ÓR	1463
Elkhorn Creek-Upper	O		T22N,R16W,S17	Men,CA	518
Elkhorn Creek-Lower	O		T22N,R16W,S17	Men,CA	518
Fox Creek	O		T22N,R16W,S21&22	Men,CA	543
Frog Pond Creek	O		T41S,R7W,S14	Jos,OR	1539
Happy Camp Creek	O		T40S,R7W S29&30	Jos,OR	1053
High Prairie	O		T14N,RIE,S21&28	Del,CA	53
Horse Linto-East	O		T7N,R7E,S7	Hum,CA	1280
Little Creek	O		T40S,R5W,S6	Jos,OR	1402
Little Greyback Crk.	O		T39S,R6W,S8	Jos,OR	1205
McKinley Creek-Lower	O		T22N,R16W,S21	Men,CA	445
Paralyze Canyon	O		T22N,R16W,S34	Men,CA	533
Skunk Creek	Ö		T22N,R16W,S29	Men,CA	529

 ^a Age-class: Y - young, M - mature, O - old.
 ^b Moisture-class: W - wet, M - mesic, D - dry.
 ^c Aquatic sites were not assigned a moisture-class.
 ^d County, State: Del - Del Norte, CA; Hum - Humboldt, CA; Jos - Josephine, OR; Men - Mendocino, CA; Tri - Trinity, CA.



Location of study sites.

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Appendix A-List of Common and Scientific Names Used in This Volume ^a

Common name	Scientific name
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INSECTS

Western spruce budworm

Choristoneura occidentalis

REPTILES

Lizards

Northern alligator lizard Sagebrush lizard Southern alligator lizard Western fence lizard Western skink

Elgaria coerulea Sceloporus graciosus Elgaria multicarinata Sceloporus occidentalis Eumeces skiltonianus

Snakes

California mountain kingsnake Common garter snake Northwestern garter snake Racer

Ringneck snake Rubber boa Sharptail snake

Western aquatic garter snake

Western rattlesnake Western terrestrial garter snake Lampropeltis zonata Thamnophis sirtalis Thamnophis ordinoides Coluber constrictor Diadophis punctatus Charina bottae Contia tenuis Thamnophis couchii Crotalus viridis Thamnophis elegans

Turtles

Western pond turtle

Clemmys marmorata

Scientific name

AMPHIBIANS

Mole Salamanders

Long-toed salamander Ambystoma macrodactylum

Northwestern salamander Ambystoma gracile

Giant and Olympic Salamanders

Cope's giant salamanderDicamptodon copeiOlympic salamanderRhyacotriton olympicusPacific giant salamanderDicamptodon tenebrosusbRocky Mountain giant salamanderDicamptodon atterimusb

Lungless Salamanders

Arboreal salamander

Black salamander

California slender salamander

Aneides lugubris

Aneides flavipunctatus

Batrachoceps attenuatus

Clouded salamander
Del Norte salamander
Plethodon elongatus
Dunn's salamander
Plethodon dunni
Ensatina
Ensatina
Ensatina eschscholtzii
Larch Mountain salamander
Oregon slender salamander
Batrachoceps wrightii

Plethodontid salamanders (lungless or woodland salamanders in the family Plethodontidae, including

Aneides spp., Batrachoceps spp., Ensatina eschscholtzii, and Plethodon spp.)

Redback salamander
Siskiyou Mountains salamander
Van Dyke's salamander
Western redback salamander
Plethodon cinereus
Plethodon stormi
Plethodon vandykei
Plethodon vehiculum

Woodland salamanders (see plethodontid salamanders)

Newts

Roughskin newt Taricha granulosa

Frogs

Cascades frog
Rana cascadae
Foothill yellow-legged frog
Rana boylii
Pacific treefrog
Red-legged frog
Rana aurora
Tailed frog
Rana aurora
Ascaphus truei

Toads

Western toad Bufo boreas

MAMMALS

Shrews

Marsh shrewSorex bendiriicMasked shrewSorex cinereusMontane shrewSorex monticolusdPacific shrewSorex pacificusTrowbridge's shrewSorex trowbridgiiVagrant shrewSorex vagransWater shrewSorex palustris

Scientific name Common name

Moles

Coast mole Scapanus orarius Shrew-mole Neurotrichus gibbsii Scapanus townsendii Townsend's mole

Bats

Big brown bat Eptesicus fuscus California myotis Myotis californicus European pipistrelle Pipistrellus pipistrellus Fringed myotis Myotis thysanodes Hoary bat Lasiurus cinereus Keen's myotis Myotis keenii Little brown myotis Myotis lucifugus Long-eared myotis Myotis evotis Long-legged myotis Myotis volans

Silver-haired bat Lasionycterus noctivagans Townsend's big-eared bat Plecotus townsendii Western small-footed myotis Myotis ciliolabrum Yuma myotis Myotis yumanensis

Rabbits and Pikas

Pika Ochotona princeps

Squirrels and Chipmunks

Douglas' squirrel Tamiasciurus douglasii Northern flying squirrel Glaucomys sabrinus Townsend's chipmunk Tamias townsendii^e Western gray squirrel Sciurus griseus Yellow-pine chipmunk Tamias amoenus

Pocket Gophers

Botta's pocket gopher Thomomys bottae Northern pocket gopher Thomomys talpoides Western pocket gopher Thomomys mazama

Mice, Rats, and Voles

Black rat Rattus rattus Bushy-tailed woodrat Neotoma cinerea California vole Microtus californicus Creeping vole Microtus oregoni Deer mouse Peromyscus maniculatus Dusky-footed woodrat Neotoma fuscipes Forest deer mouse Peromyscus oreasf Heather vole Phenacomys intermedius Long-tailed vole Microtus longicaudus Montane vole Microtus montanus Pinon mouse Peromyscus truei Red-backed voles Clethrionomys spp. Red tree vole Arborimus longicaudus⁸ Clethrionomys gapperi

Southern red-backed vole Townsend's vole Microtus townsendii

Scientific name

Mice, Rats, and Voles-continued

Water vole
Western red-backed vole
White-footed mouse

Microtus richardsoni
Clethrionomys californicus
Arborimus albipesi

Jumping Mice

Pacific jumping mouse Zapus trinotatus
Western jumping mouse Zapus princeps

Carnivores

CoyoteCanis latransErmineMustela ermineaFisherMartes pennantiGrizzly bearUrsus arctosMartenMartes americanaWolfCanis lupus

Ungulates

Elk Cervus elaphus

Mountain goat Oreamnos americanus

Mule deer Odocoileus hemionus

White-tailed deer Odocoileus virginianus

BIRDS

Swans, Geese, and Ducks

Bufflehead Bucephala albeola
Barrow's goldeneye Bucephala islandica
Common merganser Mergus merganser
Hooded merganser Lophodytes cucullatus
Wood duck Aix sponsa

Hawks and Vultures

Bald eagleHaliaeetus leucocephalusCooper's hawkAccipiter cooperiiNorthern goshawkAccipiter gentilisRed-shouldered hawkButeo linneatusSharp-shinned hawkAccipiter striatusTurkey vultureCathartes aura

Grouse and Quail

Blue grouse Dendragapus obscura
California quail Callipepla californica
Capercaillie Tetrao urogallus
Mountain quail Oreortyx pictus
Ruffed grouse Bonasa umbellus

Murrelets

Marbled murrelet Brachyramphus marmoratus

Pigeons and Doves

Band-tailed pigeon Columba fasciata
Mourning dove Zenaida macroura

Owls

Barred owl
Flammulated owl
Otus flammeolus
Otus flammeolus
Northern pygmy-owl
Northern saw-whet owl
Northern spotted owl
Strix occidentalis caurina

Scientific name

Western screech-owl Otus kennicottii

Hummingbirds and Swifts

Allen's hummingbird

Anna's hummingbird

Rufous hummingbird

Vaux's swift

Selasphorus rufus

Chaetura yauxi

Kingfishers

Belted kingfisher Ceryle alcyon

Woodpeckers

Acorn woodpecker Melanerpes formicivorus Downy woodpecker Picoides pubescens Hairy woodpecker Picoides villosus Ivory-billed woodpecker Campephilus principalis Northern flicker Colaptes auratus Pileated woodpecker Dryocopus pileatus Red-breasted sapsucker Sphyrapicus ruber Red-cockaded woodpecker Picoides borealis White-headed woodpecker Picoides albolarvatus

Flycatchers

Ash-throated flycatcher

Dusky flycatcher

Hammond's flycatcher

Olive-sided flycatcher

Western flycatcher

Western wood-pewee

Myiarchus cinerascens

Empidonax oberholseri

Empidonax hammondi

Contopus borealis

Epidonax difficilis

Contopus sordidulus

Jays, Crows, and Ravens

American crow
Common raven
Corvus brachyrhynchos
Corvus corax
Gray jay
Perisorius canadensis
Scrub jay
Aphelocoma coerulescens
Steller's jay
Cyanocitta stelleri

Chickadees, Nuthatches, and Creepers

Black-capped chickadee
Brown creeper
Brown-headed nuthatch
Chestnut-backed chickadee
Mountain chickadee
Red-breasted nuthatch
White-breasted nuthatch

Brown-headed nuthatch
Sitta pusilla
Parus rufescens
Parus gambeli
Sitta canadensis
Sitta canadensis
Sitta carolinensis

Scientific name

Wrens

Bewick's wrenThryomanes bewickiiHouse wrenTroglodytes aedonWinter wrenTroglodytes troglodytes

Kinglets

Golden-crowned kinglet Regulus satrapa
Ruby-crowned kinglet Regulus calendula

Thrushes

American robin

Hermit thrush

Swainson's thrush

Townsend's solitaire

Varied thrush

Townsend's solitaire

Varied thrush

Turdus migratorius

Catharus guttatus

Catharus ustulatus

Myadestes townsendi

Ixoreus naevius

Bushtits and Wrentits

Bushtit Psaltriparus minimus Wrentit Chamaea fasciata

Vireos

Hutton's vireo Vireo huttoni
Solitary vireo Vireo solitarius
Warbling vireo Vireo gilvus

Wood Warblers

Bachman's warbler Vermivora bachmanii Black-throated gray warbler Dendroica nigrescens Golden-winged warbler Vermivora chrysoptera Hermit warbler Dendroica occidentalis McGillivray's warbler Oporornis tolmiei Nashville warbler Vermivora ruficapilla Orange-crowned warbler Vermivora celata Swainson's warbler Lymnothlypis swainsonii Townsend's warbler Dendroica townsendi Wilson's warbler Wilsonia pusilla Yellow-rumped warbler Dendroica coronata

Tanagers

Western tanager Piranga ludoviciana

Sparrows

Bachman's sparrowAimophila aestivalisChipping sparrowSpizella passerinaDark-eyed juncoJunco hyemalisFox sparrowPasserella iliacaLazuli buntingPasserina amoenaRufous-sided towheePipilo erythrothalmusSong sparrowMelospiza melodia

Scientific name

Blackbirds, Cowbirds, and Orioles

Brown-headed cowbird

Northern oriole

Red-winged blackbird

White-winged crossbill

Molothrus ater
Icterus galbula
Agelaius phoeniceus
Loxia leucoptera

Finches

Black-headed grosbeak Pheucticus melanocephalus Evening grosbeak Coccothraustes vespertinus

Pine siskin

Purple finch

Red crossbill

White-winged crossbill

Carduelis pinus

Carpodacus purpureus

Loxia curvirostra

Loxia leucoptera

CONIFEROUS TREES (SOFTWOODS)

Yews

Pacific yew Taxus brevifolia

Pines

Jeffrey pine Pinus jeffreyi
Knobcone pine Pinus attenuata
Lodgepole pine Pinus contorta
Pinyon pine Pinus edulis
Ponderosa pine Pinus ponderosa
Sugar pine Pinus lambertiana
Western white pine Pinus monticola

Spruces

Black sprucePicea marianaEngelmann sprucePicea engelmanniiSitka sprucePicea sitchensisWhite sprucePicea glauca

Hemlocks

Mountain hemlock Tsuga mertensiana Western hemlock Tsuga heterophylla

True Firs

California red fir
Grand fir
Noble fir
Pacific silver fir
Subalpine fir
Abies amabilis
Abies amabilis
Abies lasiocarpa
Abies spp.
White fir
Abies concolor

Douglas-firs

Douglas-fir Pseudotsuga menziesii

Redwoods

Redwood Sequoia sempervirens

Scientific name

Cedars

Alaska-cedar Chamaecyparis nootkatensis Incense-cedar Libocedrus decurrens Port-Orford-cedar Chamaecyparis lawsoniana

Western redcedar Thuja plicata

FLOWERING TREES (HARDWOODS)

Bigleaf maple Acer macrophyllum Bitter cherry Prunus emarginata Black cottonwood Populus trichocarpa California black oak Quercus kelloggii California-laurel Umbellularia californica Canyon live oak Quercus chrysolepis Cascara buckthorn Rhamnus purshiana Golden chinkapin Castanopsis chrysophylla Oregon ash Fraxinus latifolia Oregon white oak Quercus garryana Pacific dogwood Cornus nuttallii Pacific madrone Arbutus menziesii Red alder Alnus rubra Scouler willow Salix scouleri

Tanoak Lithocarpus densiflorus Vine maple

Acer circinatum

SHRUBS AND HERBS

Alaska huckleberry Vaccinium alaskaense

Blackberry Rubus spp. California hazel Corylus cornuta Canadian thistle Cirsium arvense Common pipsissiwa Chimaphila umbellata Dwarf rose Rosa gymnocarpa Fireweed Epilobium spp. Hedge-nettle Stachys cooleyae Huckleberry Vaccinium spp. Little pipsissiwa Chimaphila menziesii Ocean-spray Holodiscus discolor Oregongrape Berberis nervosa Oregon oxalis Oxalis oregana

Pacific rhododendron Rhododendron macrophyllum

Pinesap Hypopitys monotropa Red huckleberry Vaccinium parvifolium Salal Gaultheria shallon Salmonberry Rubus spectabilis Thimbleberry Rubus parviflorus

Thin-leaved huckleberry Vaccinlum membranaceum

Twinflower Linnaea borealis

FERNS

Bracken fern Pteridium aquilinum Swordfern Polystichum munitum

Common name	Scientific name
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FUNGI

Red-brown butt rot White pine blister rust Phaeolus schweinitzii Cronartium ribicola

- ^b Formerly *D. ensatus*; species' revisions based on Good (1989).
- ^c Also known as Pacific water shrew.
- ^d Also known as dusky shrew.
- ^e Proposed revision of Townsend's chipmunk into four species including the Siskiyou chipmunk (*Tamias siskiyou*) is not recognized.
- f Also known as Columbian mouse.
- g Inclusion of the red tree vole and white-footed vole in the genus *Phenacomys* is not recognized.

^a Except as noted below, common and scientific names follow Collins 1990 for amphibians and reptiles, Jones and others 1986 for mammals, American Ornithologists' Union 1983 for birds, and Hitchcock and Cronquist 1973 for plants.